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A TEMNOSPONDYLOUS LABYRINTHODONT FROM THE LOWER CARBONIFEROUS

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ABSTRACT

An amphibian skull and partial skeleton from the basal part of the Mauch Chunk Group of the Mississippian of West Virginia is that of a colosteid temnospondyl described as *Greererpeton burkemorani* gen. et sp. nov.

INTRODUCTION

Although amphibian remains are plentiful in the late Carboniferous (the Pennsylvanian Period of American terminology), they are exceedingly rare in the earlier Carboniferous (the Mississippian). In this paper there is described for the first time a labyrinthodont amphibian skull from the Mississippian of North America. Until recent decades Lower Carboniferous amphibian remains were absolutely unknown except in Scotland, and even there specimens were few. All materials of that age then available were described by Watson in 1929. Once there are excluded certain specimens now known to be Upper rather than Lower Carboniferous in age (Panchen and Walker, 1961), the list of finds is a meager one. There are a few lepospondyls, mainly "adelospondyls" of Watson's terminology; of labyrinthodonts, one skeleton *(Pholidogaster)*; seven skulls, most of the peculiar loxommid type, with keyhole-shaped orbits; a few fragmentary remains.

In North America, no Mississippian amphibians were known until relatively recently. In 1941, I reported the discovery of remains of amphibians in the Hinton Formation of the Mauch Chunk Group in West Virginia; the bones present, however, were disarticulated and generally fragmentary, and hence of little morphological or evolutionary value. In 1955 I decided to initiate a new series of attempts to find sites and materials of American Carboniferous amphibians. Considerable Pennsylvanian material was found, but the only earlier find of value was that of a jaw of very late Mississippian age, apparently of an anthracosaur, in the Point Edwards Formation of the Canso Group in Nova Scotia (Romer, 1958). Further exploration for Carboniferous amphibians has been continued with success by Dr. Baird of Princeton and Dr. Carroll of McGill, principally in Nova Scotia. Again, however, their finds have been mostly Pennsylvanian, and the only Mississippian specimen reported is a partial skull of the loxommid from the Point Edwards Formation (Baird, 1962).

Of especial interest for some time, in the Lower Carboniferous of the Allegheny region, has been a quarry at Greer, West Virginia. On several occasions this was visited by parties from the Museum of Comparative Zoology; amphibian material was found, but of a fragmentary nature. More successful have been Mr. John J. Burke and Mr. William E. Moran who had earlier searched intensively in the "tri-state area" of West Virginia-Pennsylvania-Ohio for Carboniferous and early Permian vertebrates (Moran, 1952; Romer, 1952). Materials collected by them at Greer, including a skeleton which is apparently anthracosaurian, are in the U. S. National Museum collections. The present specimen from Greer not only forms an addition to our sparse representation of Lower Carboniferous labyrinthodonts, but also is important because it increases our knowledge of the stratigraphic distribution of labyrinthodont types.

In his classic papers of 1919 and 1926, Watson, for the first time, sorted out the then chaotic array of labyrinthodonts into a reasoned series of subgroups. The Triassic members, he pointed out, form the Stereospondyli, with intercentra enlarged and pleurocentra generally absent. These are clearly derivable from the Rhachitomi, abundant in the Permian, in which in each segment there were paired small pleurocentra and a fairly large intercentrum. The only type of Carboniferous vertebrae known to Watson were of the embolomere type, in which both intercentrum and pleurocentra form complete rings. He therefore concluded that the embolomeres were the ancestral labyrinthodonts, and that the evolutionary sequence ran: embolomeres — rhachitomes — stereospondyls.

This, when Watson proposed it, seemed a reasonable arrangement. But with the passage of time and augmented knowledge of fossil labyrinthodonts, the Watson classification became increasingly unsatisfactory. Therefore, I proposed (Romer, 1947) a different phylogenetic scheme, with the labyrinthodonts arrayed dichotomously in two major subdivisions, Temnospondyli and Anthracosauria. Since vertebrae similar to the rhachitomous type are found among the ancestral crossopterygians, I suggested that this was the basic vertebral structure among labyrinthodonts, and that a main central group of these forms, to be termed Temnospondyli, continued on as Rhachitomi through the Carboniferous and Permian, to terminate in the Stereospondyli of the Triassic. A major side branch, to be termed the Anthracosauria, consisted of forms in which, in contrast to temnospondyls, the small paired pleurocentra of ancestral types became enlarged and fused to form a solid ring-shaped centrum. Here the major evolutionary line led, with eventual reduction of the intercentrum, to the Reptilia, with the Seymouriamorpha as a morphologically transitional group; the Embolomeri, instead of being truly primitive forms, appear to be an anthracosaurian side branch in which the intercentrum forms a complete ring, as do the pleurocentra.

When my scheme of labyrinthodont classification was first proposed, its base in actually known materials was none too secure, mainly because of the dearth of pre-Pennsylvanian finds. However, over the last two decades new studies and new finds have tended increasingly to support it. The description of postcranial remains of the late Devonian ichthyostegids (Jarvik, 1952) strengthens the conclusion that the rhachitomous vertebral type is primitive among amphibians. Restudy of *Pholidogaster* from the Lower Carboniferous of Scotland (Romer, 1964) beautifully illustrates a stage demanded by theory in the development of the pleurocentra toward the "holospondylous" condition of advanced anthracosaurians.

There still remained, however, a major gap in the early history of the Temnospondyli. Rhachitomes, contrary to Watson's earlier beliefs, are now known (mainly through studies by Baird and Carroll) to have been abundant and varied in the Pennsylvanian, but were long thought to be absent in the early Carboniferous. At the time I proposed the phylogenetic scheme here followed, I suggested that the peculiar loxommids, present in the early as well as late Carboniferous, were rhachitomous rather than embolomerous, as Watson had believed. This has since been shown by Baird (1957) to be the case. But surely other rhachitomes in addition to the aberrant loxommids, with their peculiar keyhole-shaped orbits, must already have been present in the Mississippian. The present find of a Mississippian rhachitome of more normal structure adds major support to the belief that the Rhachitomi were already flourishing in early Carboniferous times.

PROVENANCE OF THE SPECIMEN

The materials here described were collected from the quarry at Greer, Monongalia County, West Virginia, by Mr. Burke and Mr. Moran; this site is a commercial limestone quarry, located on Deckers Creek, about 6½ miles southeast of Morgantown. The quarry region has been described by Tilton (1928), Coryell and Sohn (1938) and McCue, Lucke and Woodward (1939). The material quarried is a massive limestone of the Greenbrier Group. Mr. Thomas Arkle, Jr. of the West Virginia Geological Survey states (written communication, Jan. 7, 1969) that this bed is identified as the Union Limestone, which at Greer Quarry is overlain by the Bluefield Formation of the Mauch Chunk Group. These determinations are in keeping with studies by Wells (1950) and Flowers (1956).

Mr. Burke informs me that the specimen is derived from the Bickett Shale of the Bluefield Formation. The base of the Bickett Shale is about 16 feet above the Union Limestone at the Greer Quarry. The specimen is probably from the lower two to three feet of the Bickett, but its exact horizon is uncertain, since the rock had fallen from the face of the quarry.

The specimen is, thus, older than the fragmentary remains from the Hinton district, derived from a horizon considerably higher in the Mauch Chunk, and still older than the Nova Scotia remains mentioned above. As noted by Weller and others (1948), correlation of Lower Carboniferous American formations and zones with those of Europe is as yet none too certain, but the Greenbrier and basal Mauch Chunk seem certainly to equate roughly with the upper part of the Viséan of European terminology, and are pre-Namurian. The oldest European Carboniferous labyrinthodonts are from the "Carboniferous Limestone", Namurian in age. (A few lepospondyls come from the earlier Oil Shale Group.) Specimens from the Greer locality thus appear to be the oldest labyrinthodonts yet known except for the East Greenland ichthyostegids.

The remains here described are in all probability those of a single individual. A principal block includes the skull and jaws with, close behind, a disarticulated series of vertebrae and ribs together with belly scales which, because of the presence of elements of the shoulder girdle and front limbs, obviously represent the anterior part of the trunk. A second series of vertebrae, ribs, and scales found to the rear of the main block appear to represent the more posterior region of the trunk. Nearby were a few other finds of limb and girdle bones, ribs and scales. Since vertebrae and scales in all cases are of the same type and since the limb and girdle elements form a nearly complete set of appropriately matching size for a single individual, it is reasonable to conclude that we are dealing with the disarticulated remains of one animal. The specimen is entered as no. 10931 in the collection of the Cleveland Museum of Natural History.

I am greatly indebted to the authorities of the Cleveland Museum of Natural History for the privilege and pleasure of describing this specimen. I also wish to acknowledge help from Mr. Thomas Arkle, Jr. and the West Virginia Geological Survey for information concerning the stratigraphy of the Greer area.

SYSTEMATIC PALEONTOLOGY

Family COLOSTEIDAE Romer, 1930

Genus **GREERERPETON**[1] gen. nov.

GREERERPETON BURKEMORANI[2] sp. nov.

Figs. 1-7

Diagnosis for genus and species: A colosteid rhachitome, similar in skull roof pattern and proportions to *Colosteus*, but with a lesser development of the anterior portions of the lateral line groove system; premaxillary "tusks" present, as in *Erpetosaurus*.

Holotype: Cleveland Museum of Natural History no. 10931.

Occurrence: Bickett Shale of the Bluefield Formation, Mauch Chunk Group, Mississippian.

Locality: Greer, Monongalia County, West Virginia, on Deckers Creek, about 6½ miles southeast of Morgantown.

Repository: Cleveland Museum of Natural History.

[1] The generic name is derived from the locality.

[2] The specific name is formed (reasonably if unorthodoxly) by combining the surnames of the two discoverers of the specimen.

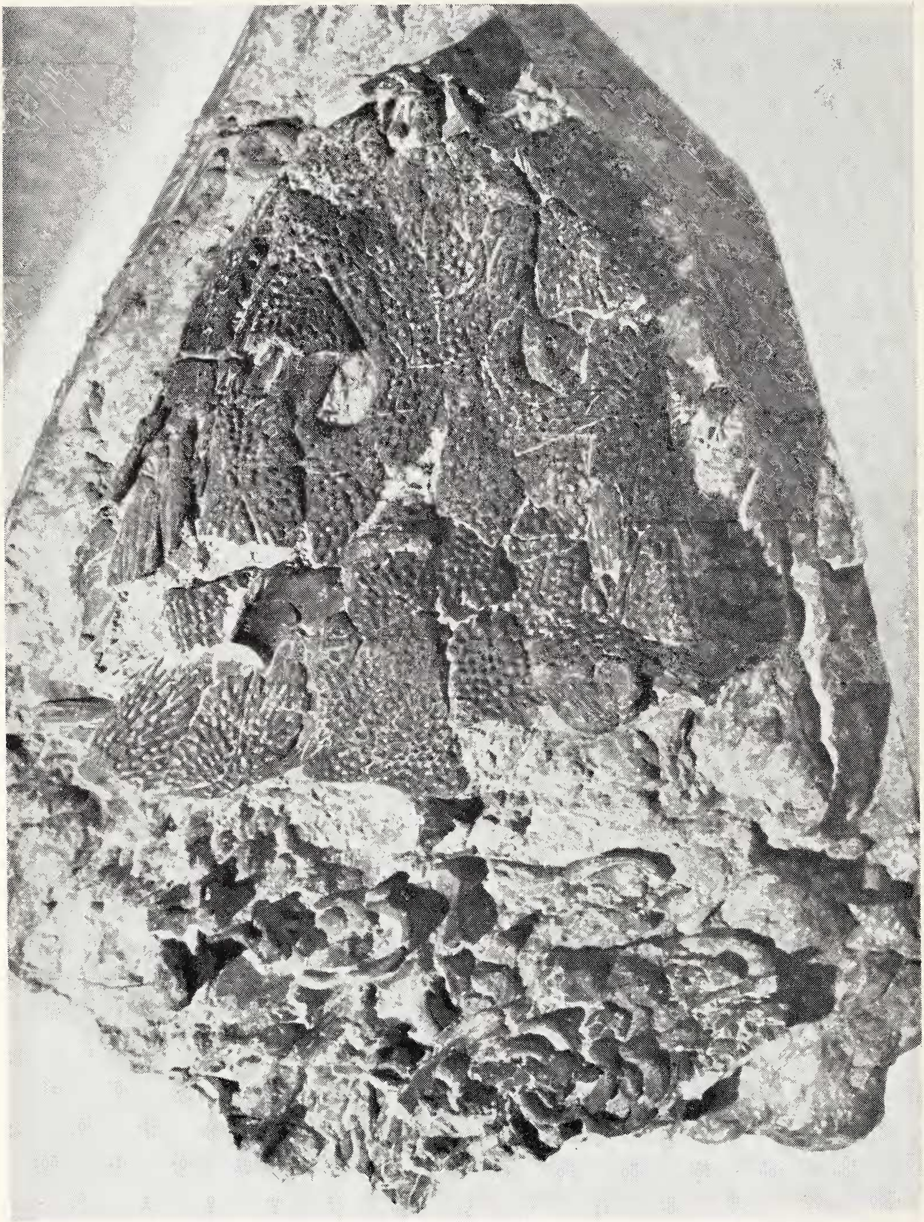

Fig. 1. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Photograph of the main block containing the skull and remains of the anterior part of the trunk, × ⅔.

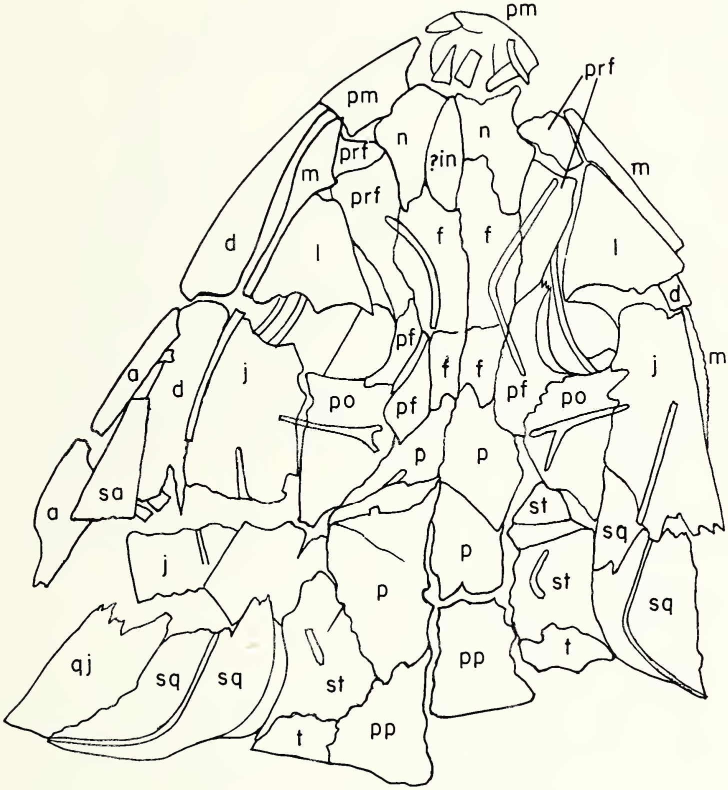

Fig. 2. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Key to elements present on the skull, as preserved: *a,* angular; *d,* dentary; *f,* frontal; *?in,* internasal; *j,* jugal; *l,* lacrimal; *m,* maxilla; *n,* nasal; *p,* parietal; *pf,* postfrontal; *pm,* premaxilla; *po,* postorbital; *pp,* postparietal; *prf,* prefrontal; *qj,* quadratojugal; *sa,* surangular; *sq,* squamosal; *st,* supratemporal; *t,* tabular, × ⅔.

DESCRIPTION

Cranial remains: The principal block (figs. 1 and 2) contains the entire cranial structure, with the skull, seen from above, crushed flat and somewhat disarticulated. Most of the left jaw ramus is seen to the left of the skull (the articular region and partial surangular were removed during preparation); the right ramus is mainly concealed by the skull, but the articular region is seen behind the right tabular. Except for the right quadratojugal and the anterior end of the left jugal, nearly the entire series of dorsal dermal elements is present. The crushing of the skull has caused considerable fracturing and disarticulation. The stoutness of the premaxillae, together with the presence of large tusks in this region, has caused these elements to be partially overturned and separated from the roofing bones posterior to them. The upward tilting of the sides of the skull into the horizontal plane has separated the lacrimals of both sides from the prefrontals, and on the left side has separated the "cheek" elements — squamosal and quadratojugal — from the table, and the left parietal, as well as the "table" elements posterior to it have been pushed some distance to the rear, together with the left "cheek".

In figure 3 I have attempted to articulate the roofing series in natural relations. Since, however, the palatal structure is almost unknown, I have been unable to determine the true width of the skull and consequently have been forced to restore the whole roof in an unnatural horizontal plane (fig. 3). As a result, the articulation between elements is to some extent distorted; more important is the fact that this type of restoration makes the skull appear considerably broader than it actually was in life.

The length, as restored, from snout to the back edge of the skull table, is 128 mm. The general proportions of the skull (allowing for the artificiality of the apparent width) are those of a moderately long and rather narrow structure. The orbits, apparently typically circular in outline, lie well toward the front of the skull, giving a relatively short face and a much elongated postorbital segment. The skull table is broad; on either side the cheeks slant backward gently toward the jaw articulation. The area of junction of cheek and table is disturbed on both sides. That the suturing was not too tight between the two regions is demonstrated by the clean break between cheek and table seen on the left. There was obviously little or no development of an otic notch.

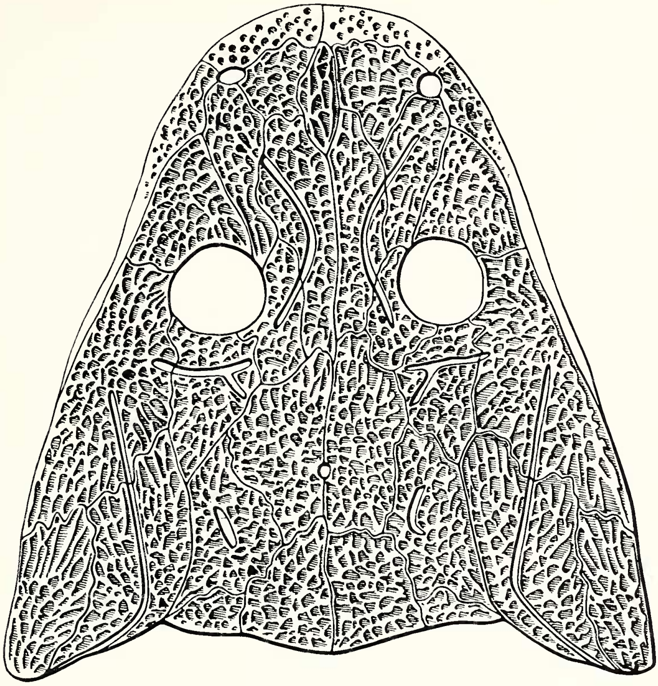

Fig. 3. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. The skull roof restored; the elements are shown as if all were in a horizontal plane, and hence the true width is exaggerated, × ⅔.

The sculpturing is of a typical labyrinthodont type: essentially circular depressions surrounded by ridges near centers of ossification, gradually changing to a series of long ridges with intervening valleys in elements which extend some distance from the ossification centers. A considerable amount of the potential pattern of grooves for lateral line canals is present. The cheek line is seen extending backward and upward on the posterior part of the jugal and anterior part of the squamosal, and then curving downward posteriorly to disappear at the posterior edge of the cheek near the squamosal-quadratojugal suture. Of the longitudinal canals originally present on the skull table, there is to be found only a pair of short grooves on the supratemporals. The supraorbital lyrae are distinctly developed on postorbitals, jugals and prefrontals. A transverse postorbital canal, forked medially, is present on both postorbitals. There is no trace of a suborbital groove although it may have been present along the suture between the (disarticulated) maxillae and the elements dorsal to them. I have seen no interpretable traces of canals such as are found on the snouts of various other labyrinthodonts.

The premaxillae are stout elements whose outer edges are considerably thickened and curve strongly downward from the level of the snout roof to the upper jaw margins. The anterior ends of the maxillae are broadened and obviously thickened dorsally; they extend as slender tooth-bearing strips far back below lacrimal and jugal. The state of preservation makes it impossible to give details of the region of the external naris; apparently premaxilla, maxilla, nasal and prefrontal enter into its borders. The lacrimal appears to have been excluded. The nasals are short but broad. Between two areas clearly belonging to the pair of nasals is a median strip of bone which I was at first inclined to consider a broken-off fragment of one of the nasals. However, the sculpture pattern of this area shows no relation to that adjacent to it on either nasal, and I think it likely that we have here an internasal, a median unpaired element such as is found occasionally in other labyrinthodonts.

The frontals are broad anteriorly, but narrow posteriorly between the orbits. The parietals are well developed, laterally occupying (with the postorbitals) the area in which intertemporals are present in many early forms. Postparietals are large and elongate.

Of the circumorbital series, the lacrimals are large, essentially triangular elements broadly exposed along the anterior margin of the orbits and tapering anteriorly; they appear not to have reached the external nares. The prefrontals are elongate, narrow posteriorly but broadening anteriorly. They appear to have but barely entered the orbital margins anterodorsally. The prefrontals extend much farther forward toward the nares than is typical of labyrinthodonts generally. About opposite the anterior tips of the lacrimals there is a crack separating the regions definitely pertaining to the prefrontals from an area running forward toward the nares. I am none too certain of the identification of the element or elements present here. Possibly the maxilla may extend medially here; possibly part or all of this area may constitute an external exposure of a septomaxilla (not otherwise identifiable in the specimen). It seems, however, more probable that we are dealing with a still further extension of the prefrontal.

The upper margins of the orbits are formed by the postfrontals, narrow anteriorly but broadening posteriorly where they extend some distance back of the orbits to reach the parietals. The postorbitals are elongate anteroposteriorly, in conformance with the general elongation of the postorbital region of the skull; they taper posteriorly to terminate between supratemporal and squamosal. The jugal is the largest in area of the dermal roofing elements, covering most of the anteroventral area of the "cheek" and extending forward broadly beneath the orbit to the lacrimal.

Of the lateral elements of the skull table, the presumably primitive intertemporal is absent. The supratemporal is a large element, its anterior end lying between parietal and postorbital; posteriorly the supratemporal tapers laterally to a point close to the otic notch region. In temnospondyl fashion the tabulars are small, bounded anteriorly by the supratemporal and medially by the postparietal; there is, of course, no tabular-parietal contact. The squamosal is broad, and rather elongate; and the quadratojugal well developed. Although the articulation of squamosal with the skull table is obviously relatively loose, as noted earlier, there can be seen a flange of the squamosal which ran medially underneath the supratemporal.

It would be an extremely difficult task to remove the skull from the thick block of impure limestone in which it is embedded; in consequence little can be said of the palate, of which a few glimpses can be had through the orbits and broken areas of the skull roof. Part of the transverse flange of the left pterygoid has pushed up to the surface in front of the left squamosal, and portions of the anterior rami of the pterygoids are visible through the two orbits. In the left orbit is seen in dorsal view the somewhat thickened margin of the bone bordering the interpterygoid vacuity. On the right the bone has apparently been broken and displaced, so that the palatal surface of the same area is seen, the margin toward the interpterygoid vacuity bearing a band of small denticles.

As mentioned above, the right jaw ramus is concealed by the skull except for the articular region. On the left the block exhibits a considerable part of the ramus, including most of the dentary and parts of angular and surangular. A posterior fragment of this jaw, removed from the block during preparation, is shown in figure 4.

Much of the dentary is visible on the left jaw ramus. At mid-length of the bone there are teeth of labyrinthine structure and modest height, spaced at intervals of about 5 mm, with frequent

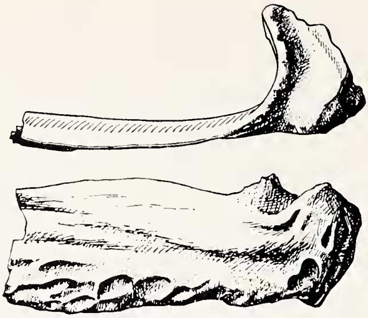

Fig. 4. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Left articular region and partial surangular in dorsal and lateral view, × 1.

empty sockets in alternate positions. As expected, tooth size and spacing decrease posteriorly. A large tooth, with a length of about 9 mm, is seen projecting downward from the posterior margin of the left premaxilla. The right premaxilla has been broken off and overturned, revealing the presence here of several large tusks, grooved in labyrinthine fashion, and with estimated lengths of well over a centimeter. Two are broken off and one or both of these may have been parasymphysial teeth of the lower jaw. One however, is definitely attached to the premaxilla — a most unusual situation for a large tooth of this sort.

Postcranial skeleton: Much of the vertebral column is present, but disarticulated; as noted above, a considerable series of vertebrae of the anterior part of the trunk is represented by materials posterior to the skull on the main block (fig. 5); a second block carries a series presumably from the posterior part of the trunk (fig. 6). The vertebral structure is typically rhachitomous. On both blocks there are numerous intercentra; a total of about 30 are clearly visible. They are stout structures although in many cases broken in two by crushing. They have a typical crescentic shape, as seen in end view; broad below, with an anteroposterior dimension of 5 to 7 mm, they taper upward on either side to form nearly a semicircle. Although moderately thick ventrally, there nevertheless remains a large cavity for the presumably persistent notochord. The curvature of the intercentra shows the diameter of the column to have been about 20 mm. The pleurocentra are less well preserved, but can be seen to have been the typical rhachitome wedge shape. A relatively few neural arches are visible. The spines are low, with

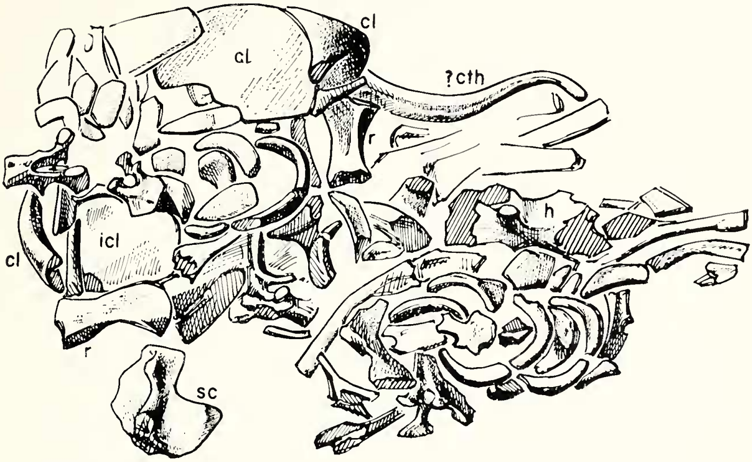

Fig. 5. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Postcranial remains present on main block: *cl,* clavicles; ?*cth,* possible cleithrum; *h,* humerus; *icl,* interclavicle; *r,* radius; *sc,* left scapulocoracoid, × ⅔.

the greatest height observed about 15 mm above the level of the zygapophyses, but are stoutly built, with transverse widths of several millimeters and anteroposterior dimensions of 5 to 7 mm. The zygapophyses diverge moderately on either side of the arch base, the width across them being 7 to 9 mm. On either side, the arch bases send broad processes down and outward ending below in horizontal surfaces for rib articulation. Scattered ribs are present; the longest seen has a length of about 40 mm. The slender shafts are nearly straight; the heads are expanded in triangular fashion.

I have not figured the abdominal scales, but a plentiful supply is present below each of the two series of vertebrae. They have the typical labyrinthodont oat-grain shape, and are generally about 10 mm in length.

As noted earlier, there was found with the specimen most of an appropriate series of limb and girdle bones (fig. 7). Those present appear to pertain to a single individual. All are of small dimensions for an animal with a skull of this size, indicating feeble limbs and an obviously aquatic habitat. As an indication of size, I may note that the femoral length is only about 25 percent of skull length, whereas in *Eryops* this figure averages about 35 percent, and in

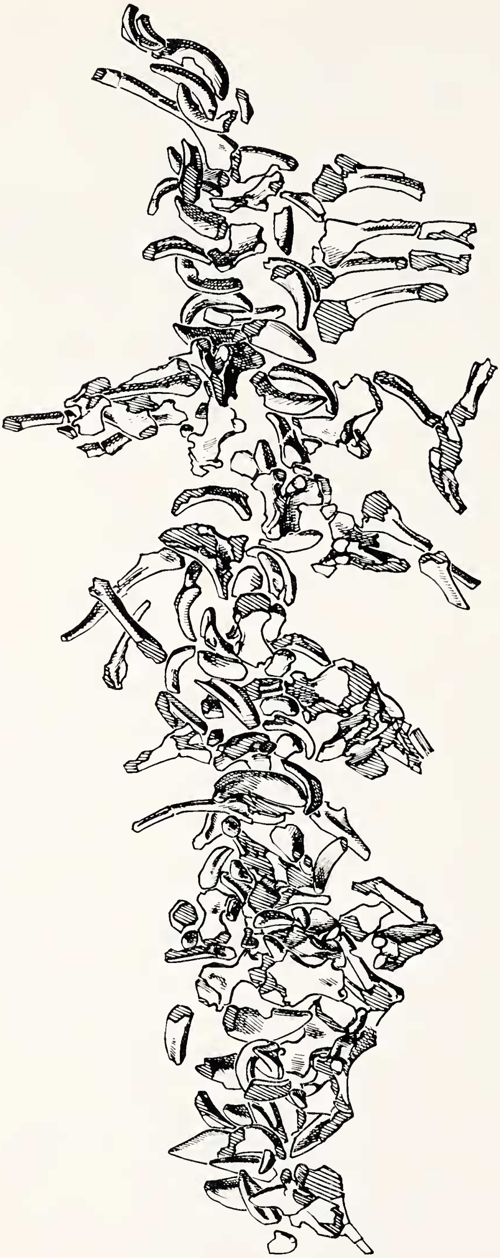

Fig. 6. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Disarticulated elements — neural arches, intercentra, pleurocentra, ribs — pertaining to posterior part of trunk, × ½.

Cacops about 55 percent. On the other hand, members of the *Trimerorhachis* group, which are known from the Pennsylvanian and early Permian, are, like the present form, small limbed. Associated materials are none too common, but in this group femoral length appears to be rather less than 25 percent of skull length. At first sight, the limb and girdle structures in the present specimen appear to be generally comparable to those of trimerorhachoids.

The dorsal ends of both clavicles are visible behind the skull in the main block, projecting upward in typical tapering fashion. Their vertical position is due to their possession of expanded lower portions lying in the plane of the block surface; the blade of the right clavicle is exposed, that of the left concealed. I have not identified cleithra, although a long slender structure lying behind the right side of the skull may be such an element. A portion of the presumably expanded interclavicle is visible near the left clavicle. A single scapulocoracoid of the left side, seen from the inner sur-

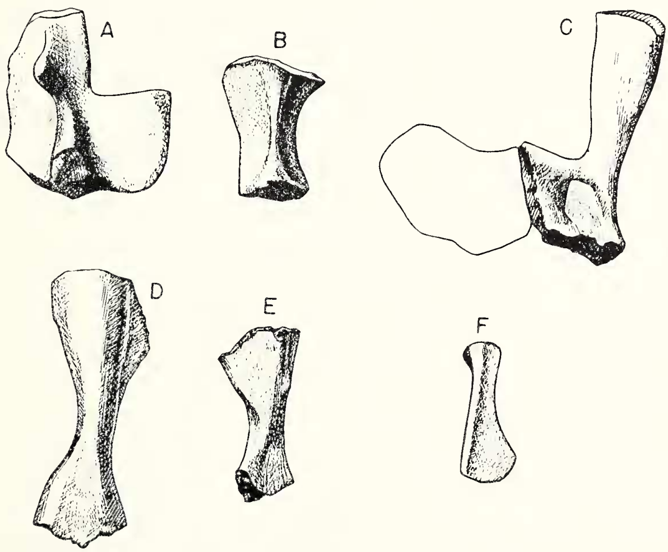

Fig. 7. *Greererpeton burkemorani* Romer, C. M. N. H. no. 10931. Limb and girdle elements. *A*, left scapulocoracoid, inner surface. *B*, right radius, flexor aspect. *C*, right ilium; ischium (seen only from inner surface) in outline. *D*, right femur, dorsal aspect. *E*, left tibia, extensor aspect. *F*, left fibula, extensor aspect, all × 1.

face, is preserved adjacent to the left clavicle. As in trimerorhachoids, most of the coracoid plate and scapular blade is unossified; the scapulocoracoid as preserved includes only the general region of the supraglenoid buttress. The preservation is poor, and I am unable to determine whether or not the typical supraglenoid foramen was present. There are remains of both humeri, but little can be made out regarding their structure. Both radii are present; they are short but broad elements about 19 mm long and in general resemble the corresponding elements of *Eryops*. The lateral margin is thin. Posteriorly, toward the median side, there is a sharp longitudinal ridge. The upper end is very broad, with a width of 11 mm; the distal width is about 8 mm. Ulnae are not well preserved, and I have not identified elements of the manus.

Both ilia are present: the right well preserved, the left imperfectly. The shape is that seen in many later rhachitomes, with a tall vertical blade, and no trace of a posterior process (not even the slight spur seen in *Eryops*). There is a typical supra-acetabular buttress. The right ilium has a total height of 30 mm. The two ischia are present. Both are seen from the concave featureless inner surface; their greatest lengths, from acetabulum to distal end, are 24 mm and 20 mm, as preserved. There is no trace of a pubis; very probably, as in various other amphibians, this bone failed to ossify.

Of hind limb elements, the femur, tibia and fibula of the left side were found associated with one another and with the left ilium; the right femur and tibia were found isolated. The left femur has a length of 40 mm; the right, apparently incomplete distally, is 35 mm long. As in temnospondyls generally the head is expanded anteroposteriorly and thin dorsoventrally. From the articular surface of the head, an unfinished surface runs downward and distally along the outturned margin of the shaft for some distance, to be continued by a pronounced ridge which extends down the anteroventral margin of the shaft to terminate at the ventral distal midpoint. There is a typically gentle groove distally between the two slightly convex condyles. There are, as usual, two distal condylar facets for the tibia, the distal face of the bone giving the appearance of a thickened V, with an apex ventrally at the termination of the ventral ridge.

The two tibiae measure 22 and 21 mm in length. As with the radius, we are dealing with a short but stout element. The head is broadened to about 11 mm for apposition to the two femoral condyles; the medial portion of the head is much the thicker of the two areas, with a depth of 6 mm. Below the medial head there is a slight development of a cnemial rugosity and crest. On the flexor aspect below the head there is a low, short but rugose longitudinal crest (a somewhat similar structure is present in *Eryops*). Below the head, the bone contracts, with a pronounced lateral convexity, to a short shaft and then, twisting somewhat laterally, expands to a distal articular surface clearly divided into separate areas for intermedium and fibulare. The distal end of the bone has a width of about 9 mm; the articular face is broadest on the facet for the fibulare, measuring here 4 mm. Except for lesser development of a cnemial crest, the whole structure of the bone resembles that of *Eryops*.

The left fibula is 18 mm long as preserved. Its proportions are those of early tetrapods in general. The upper end is about 3 mm wide; the broadened lower end has a width of about 7 mm. There are no identifiable remains of the pes.

DISCUSSION

That the amphibian here described was primarily a water-dwelling form rather than one leading a truly amphibious existence, seems clear from the small limbs, which were obviously incapable of supporting the body and heavy head on any extensive forays onto land, and from the developed series of grooves indicating a functioning lateral line system. A primarily aquatic existence in early Carboniferous amphibians generally is to be expected (the rather well developed limbs of ichthyostegids are a puzzling exception) in the seeming absence of a terrestrial food supply of animal nature before the radiation of insects in the Pennsylvanian.

Of greater interest, however, is the determination of the systematic position of this Mississippian form and its position in labyrinthodont evolution. Previously the only known Lower Carboniferous temnospondyls had been the obviously aberrant loxommids. We have here a form with orbits of normal shape, rather than the peculiarly elongate openings of the loxommids, and I fondly hoped at first, that the present form might prove to be a "generalized" rhachitome, close to the ancestor of the abundant rhachitomous amphibians of the Pennsylvanian and early Permian.

This, sadly, proves not to be the case. Typical later rhachitomes (except for short-skulled types) have orbits posterior to the midpoint of the skull length; here the eyes are well forward, with a relatively short face and a long postorbital region. A shortness of face combined with relatively small limbs suggests the trimerorhachoid rhachitomes — a group which, although off the main line toward typical advanced rhachitomes and stereospondyls, nevertheless must have branched off at an early and primitive stage, since they preserved the primitive movable basal articulation of braincase and palate and retained the intertemporal element. When, however, the skull was reassembled, this possibility disappeared, for there is no intertemporal.

Further thought and search led to the true but unexpected determination of the specimen's position. We have here a predecessor of the Colosteidae, a small group of Pennsylvanian temnospondyls of problematical relationships, whose members (*Erpetosaurus* and *Colosteus*) were described by Romer (1930) and by Steen (1931).

In every known regard the present form shows agreement with the two colosteid genera. The general skull proportions with a short face and a long postorbital region, are identical. Here, as in *Colosteus,* but in contrast to typical labyrinthodonts, there is no development of a marked otic notch. The pattern of the lateral line canals in our specimen is similar to that seen in *Colosteus,* except that the anterior portions of the system are not as well developed (as far as can be determined) as in the Pennsylvanian forms. Here, as in the colosteids, the lacrimal enters broadly into the orbital margin and tapers anteriorly, whereas in typical temnospondyls this bone enters the orbit only over a short stretch and is often completely excluded. The remarkable forward extension of the prefrontal found here is also characteristic of colosteids, and contrasts with the situation found in most labyrinthodonts. The pattern here of the long postorbital segment of the skull (with the intertemporal absent) agrees well with that of the colosteids. To some degree a similar pattern is present in other temnospondyls in which the posterior part of the skull is lengthened, but the high development of postparietals and supratemporals, in contrast with much reduced tabulars, is notable.

It is obvious that in this new form the palate, although little of it is visible, was widely open, as in colosteids, and one may expect that here, as in that family, the movable basal articulation of braincase and palate had been preserved. The most definitive point of resemblance has to do with the presence, both in our form and in the colosteids, of large tusks near the tip of the snout — a situation unknown elsewhere among temnospondyls. The distribution of the large anterior teeth in *Colosteus* is not known in detail, but in *Erpetosaurus,* as figured by Steen (1931, figs. 4, 5) there are large tusks on the premaxilla, and in the present specimen at least one such premaxillary tusk is present.

Our new form, then, is definitely attributable to the Colosteidae. It is of interest in showing that this family, formerly known from the Pennsylvanian alone, is of great antiquity. But such attribution does not place it with any degree of assurance in the general picture of temnospondyl radiation, for the colosteids are themselves a problematical group. When the ichthyostegids were first described by Säve-Söderbergh (1932) I jumped to the conclusion, based on the general skull pattern, that *Otocratia* of the Mississippian and the colosteids of the Pennsylvanian were ichthyostegid relatives (Romer, 1947). The assumption that *Otocratia* is indeed related seems to be confirmed by the finding of ichthyostegids with comparable otic peculiarities (Jarvik, 1952), but that the colosteids are also ichthyostegids is very doubtful. Apart from general skull proportions and the loss of the intertemporal, there is at present no reason to claim relationships, and it seems more probable that the colosteids were, rather, an early offshoot of the Rhachitomi, paralleling the trimerorhachoids in skull proportions, small limbs, retention of a movable basal articulation and opening up of large interpterygoid vacuities, but differing in loss of the intertemporal.

Our present specimen does not, thus, furnish us with a potential ancestor of the typical rhachitomes of later times. But the presence in the Mississippian of such an unusual type, together with the equally aberrant loxommids, indicates that the radiation of the Rhachitomi was well under way in early Carboniferous times. Should future exploration, hopefully, result in additional finds of Mississippian labyrinthodonts, we may expect that there will be found in the faunal assemblages not only representatives of progressive stages in anthracosaurian evolution but also specimens demonstrating an active radiation of early rhachitomes.

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